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INTER-HABITAT VARIATION IN THE BENTHOS OF THE UPPER MISSOURI RIVER (NORTH DAKOTA, USA): IMPLICATIONS FOR GREAT RIVER BIOASSESSMENT†

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ABSTRACT

We examined inter-habitat variation in benthic macroinvertebrate assemblages in the 180-km Garrison Reach of the Upper Missouri River, North Dakota (USA) in 2001–2003. The Garrison Reach is unchannelized with a mostly rural setting. Flows are regulated by Garrison Dam. We sampled benthos from three habitats defined *a priori*: channel, shoreline, and backwater. Benthic assemblages were different in each habitat. Average Bray-Curtis dissimilarity in assemblage composition ranged from 89% for backwater versus channel habitat to 70% for backwater versus shoreline habitat. There were distinct intra-habitat groups within *a priori* habitats: channel assemblages included moving-sand assemblages and other-substrate channel assemblages; backwater assemblages included connected (to the river channel) and unconnected backwater assemblages; shorelines assemblages varied between natural (unprotected) and riprap (rock revetment) shorelines. Abundance and taxa richness were lowest and spatial variability highest for moving-sand channel assemblages. Abundance was highest in backwaters. Taxa richness in backwaters and along channel shorelines were similar. Assemblages in all three habitats were dominated by Nematoda, Oligochaeta and Chironomidae. Taxa in these groups comprised at least 80% of mean abundance in all three habitats. Taxa that discriminated among habitats included the psammophilic chironomid *Chernovskiia* for moving-sand channel substrates versus all other habitats; *Hydroptila* (Trichoptera) for riprap vs natural shorelines, *Aulodrilus* (Oligochaeta) for connected versus unconnected backwaters; and Nematoda for backwater versus channel and shoreline versus channel. Based on overlap patterns in benthic assemblages among habitats, we concluded that sampling main channel shorelines should also capture much of the natural and stressor-induced variation in connected backwater and channel habitat exclusive of moving-sand channel habitat. Published in 2006 by John Wiley & Sons, Ltd.

KEY WORDS: Great Rivers; Missouri River; benthos; benthic macroinvertebrates; EMAP; backwater; bioassessment

INTRODUCTION

The U.S. Environmental Protection Agency's Environmental Monitoring and Assessment Programme (EMAP) is a national research effort supporting state-based efforts to determine status and trends in the ecological condition of aquatic ecosystems of the United States, including wadeable streams, rivers, lakes and coastal ecosystems (McDonald *et al.*, 2004, USEPA, 2005). EMAP is now addressing assessment of the largest rivers in the central basin of the United States. These 'Great River' ecosystems (GREs) include the Missouri, Mississippi and Ohio Rivers.

Great River hydroscapes include multiple aquatic habitats (e.g. the main channel, anabranches or chutes, islands, backwaters, riparia, floodplain lakes, tributary and reservoir deltaic zones, reservoirs and pools) that vary in regulatory jurisdiction, ecosystem services they provide, and probably in sensitivity of their fauna to each class of anthropogenic disturbance (Schweiger *et al.*, 2004). Within their main channels, large rivers exhibit physical and hydraulic transverse zonation among thalweg and lower-current-velocity lateral and shoreline habitats that influences the distribution of many groups of organisms (Stalnaker *et al.*, 1989; Bournaud *et al.*, 1998). From the perspective of bioassessment sample design, each Great River habitat can be (i) considered distinct and sampled as

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a discrete population of sites, (ii) combined with other habitats or (iii) explicitly omitted from the design (Bolgrien *et al.*, 2004; Schweiger *et al.*, 2004). Deciding which habitats to include in a sample design, and how to collect samples in each is an important early step in designing a Great River monitoring and assessment programme (Reash, 1999).

In this paper, we report on the initial GRE research: a study on the Upper Missouri River designed to evaluate sample designs and methods (Bolgrien *et al.*, 2004; Schweiger *et al.*, 2004), and to explore natural and anthropogenic sources of variation in biological indicators of condition including benthic macroinvertebrate assemblages (benthos). In this paper we examine inter- and intra-habitat variation in the benthos of the Upper Missouri River in North Dakota, USA.

STUDY REACH AND METHODS

Study reach

The Garrison Reach of the Upper Missouri River flows through central North Dakota (Figure 1). The 180-km long reach is defined as free-flowing river between Garrison Dam and Lake Oahe. Our study reach extends from

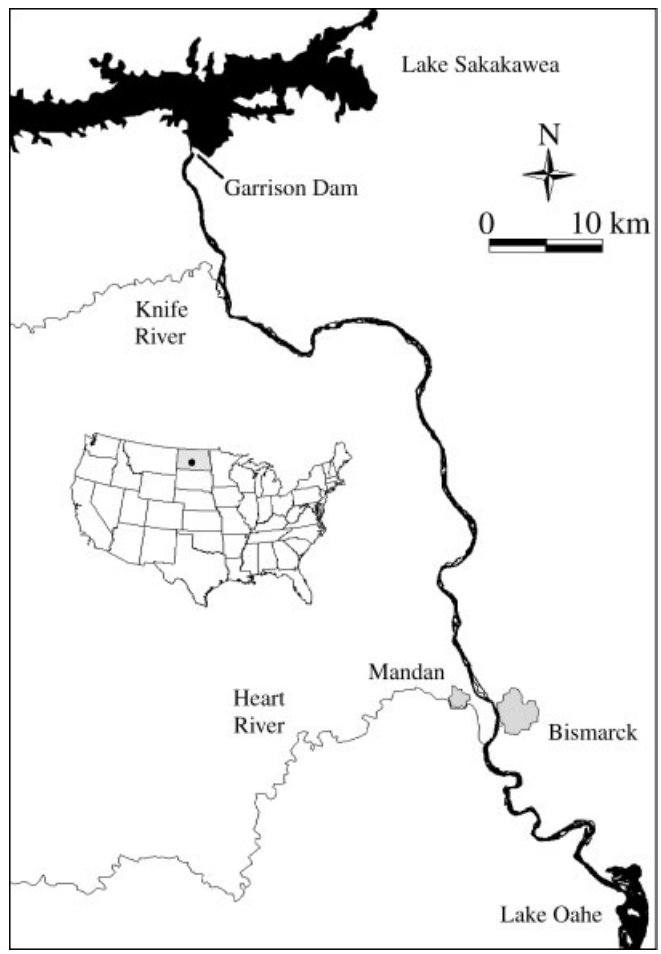

Figure 1. Map of the Garrison Reach of the Missouri River in North Dakota showing the location of Garrison Dam, the cities of Bismarck and Mandan, and Lake Oahe. Inset map shows location of the reach in North Dakota and the United States. Two significant tributaries enter from the west, the Knife River (RK 2213; 4.2 $m^3 s^{-1}$ median discharge), and the Heart River (RK 2110; 5.8 $m^3 s^{-1}$ median discharge; USGS, 2004)

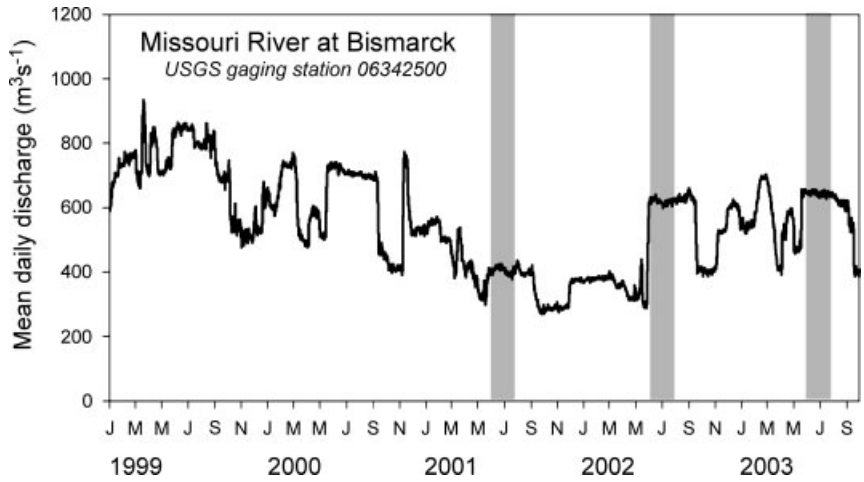

Figure 2. Mean daily discharge in the Missouri River at Bismarck, ND, 1999–2003. Shaded bars indicate when we collected samples. Flows are controlled at Garrison Dam

the dam at RK (river kilometres from the mouth) 2237, downriver to RK 2060. The river flows between the cities of Bismarck and Mandan (combined population of about 73 000; USCB, 2000), but otherwise the surrounding landscape is rural. The transition from Missouri River into Lake Oahe occurs at about RK 2070. This zone (RK 2070–2060) is referred to herein as the Lake Oahe delta. Median annual discharge at Bismarck for the period of record was $629\,m^3\,s^{-1}$ (USGS, 2004). Since completion of the dam in 1953, discharge has not exceeded the channel capacity of $1840\,m^3\,s^{-1}$ (NDGFD, 1998). Summer base flows were lower in the first year of sampling (Figure 2), but no extreme flow events occurred during or between sampling periods (June–August; 2001–2003) (USGS, 2004).

The river flows through an alluvial valley that ranges in width from <1.6 km near Garrison Dam to >11 km south of Bismarck (Figure 1). Alluvial bank materials in the reach are composed of weakly-cohesive sandy-silt (Berkas, 1995). Much of the channel has a moving-sand bed (bed $D_{50} = 0.92$ mm, Biedenharn *et al.*, 2001). Bed degradation of 1.5 to >3 m has occurred for at least 40 km below the dam (Williams and Wolman, 1984; Biedenharn *et al.*, 2001) resulting in substrate coarsening (T.R. Angradi, personal observation). Mean channel depth was about 2 m during the study (Appendix). Mean bank-full width in the reach is 615 m (Biedenharn *et al.*, 2001). About 25% of the main-channel shoreline above RK 2090 is stabilized with blanket rock revetment ('riprap') or other revetments (Angradi *et al.*, 2004). Gravel and cobble colluvium eroded from the river bluff naturally armors another 9% of the shoreline (Angradi *et al.*, 2004). Although the influence of the dam decreases down-river through the reach, we consider the entire reach to be a reservoir tailwater environment with flow, thermal and sediment regimes, aquatic habitat and water quality much altered relative to pre-dam conditions (Schmulbach *et al.*, 1992; NDGFD, 1998; NRC, 2002).

Habitats

We selected three habitats: channel, shoreline and backwater, in which to examine inter- and intra-habitat variation in benthos. We defined channel habitat as all channels within the banks defined by the pre-dam floodplain margin, excluding tributaries, between the dam and RK 2060. Except for a few downriver sites in the Lake Oahe delta, all channel sites were in moving water. We defined shoreline habitat as the wadeable margin of the main channel or anabranch nearest to the pre-dam floodplain margin between the dam and RK 2070, including natural shorelines and shorelines blanketed with riprap. We did not extend the shoreline population into the Lake Oahe delta because main-channel shorelines in the delta are not well defined. We defined backwaters as any enclosed or semi-enclosed lentic habitats between the dam and RK 2070 situated within the high banks defined by the pre-dam floodplain margin. Garrison Reach backwaters are formed behind artificial structures, such as jetties or wing-dikes,

or by fluvial action in the case of scour holes on bars and cut off secondary channels. All backwaters sampled were within 500 m of the river. We did not extend the backwater population into the Lake Oahe delta because all aquatic habitats in the delta were more or less contiguous. We developed a GIS-based representation of habitats in the reach by delineating habitat polygons on color-infrared aerial imagery and digital ortho-photos. We used EMAP design algorithms applied to this representation of the river to generate random sample locations in each habitat (see Schweiger *et al.*, 2004 for more details).

Field and laboratory methods

We collected samples at 36 randomly-located sites in each habitat during the study period (June–August, 2001–2003). We selected and sampled additional non-random sites to increase the range of environmental conditions in the data. Total sample sizes are given in results. We revisited about 10% of the sites during each field season to evaluate intra-annual between-visit variation (a surrogate for all sources of intra-seasonal variation). Revisits were 2–6 weeks apart.

At each backwater site, we collected five replicate samples with a standard PONAR dredge (483 cm^2) from a boat if the backwater was navigable and by wading if not. We collected channel samples from the boat using the same gear. We repositioned the winch boom between replicates to avoid superposition of PONAR samples. We collected five replicate shoreline kick-net samples (0.5 mm mesh, 930 cm^2) spaced 10 m apart along the shoreline and centered on the coordinates for the site.

We elutriated the five replicates for each site in the field to remove as much material <0.5 mm as possible and combined them to form a single composite sample for each site. Elutriation was achieved by using a large ($\approx$40 L) tilting basin draining into a mesh sleeve (0.5 mm mesh openings) and reservoir bottle. Water was added to the basin and the contents agitated by hand. The basin was tilted to drain and all suspended material >0.5 mm was captured in the sample bottle. The process was repeated until the basin was empty or contained only coarse sand and gravel. The composite sample was preserved in 10% formalin. Composite samples were subsampled using a gridded tray. Randomly-selected grids were picked under magnification until 300 organisms were removed. Organisms were identified, usually to genus, although many immature specimens could be identified no further than family. All organisms were sorted from samples that had fewer than 300 organisms. Ten percent of the samples from each batch of processed samples were re-picked. If the total count was $>110\%$ of the original count, the entire batch was re-picked.

While at anchor over the site, we determined current velocity 0.5 m above the river bed at channel sites with a Price type-AA current meter. Other measurements included depth (channel and backwater sites), dominant substrate determined from PONAR contents or by direct observation (converted to phi [ϕ] scale for analysis; ϕ is the negative log of the particle diameter in mm), backwater type (connected to the river or not), backwater surface area, shoreline bank angle and a subjective human disturbance rating for each backwater (a weighted sum of all the disturbances observed in the floodplain 'watershed' of the backwater).

At all sites, we determined dissolved oxygen, water temperature, and conductivity at the surface, and we collected a water sample for turbidity and flourometric chlorophyll *a* determination. At channel and backwaters sites, we collected a water sample for determination of nutrients, dissolved metals and anions, chlorophyll *a* and total suspended solids. Chemical analyses were conducted at the USEPA laboratory in Golden, Colorado and at the USEPA Mid-Continent Ecology Division Laboratory in Duluth, Minnesota using USEPA-approved methods.

Analysis

We analyzed assemblage data using the Plymouth Routines in Multivariate Ecological Research (PRIMER version 5, Clarke and Gorley, 2001). We used correlation-based principal components analysis (PCA) to ordinate sample sites using normalized environmental data including substrate size and field and laboratory water quality measurements. Normal probability plots showed that many environmental variables required log-transformation prior to PCA.

Two-dimensional ordinations of benthos samples were based on non-metric multidimensional scaling (MDS) of Bray-Curtis similarity matrices of fourth-root transformed macroinvertebrate densities. Fourth-root transformation down-weights the influence of abundant taxa to focus on contributions to patterns in the assemblage by both

common and rare species (Clarke and Warwick, 2001). Standardization of the data to a total abundance of 100 organisms for each sample was appropriate as a partial remedy for the unknown variation in the data resulting from different methods (i.e. kick sampling versus PONAR sampling), and from variation in sampling efficiency among habitats and between sites within habitats that varied with depth, substrate, or current velocity (Clarke and Warwick, 2001).

We determined contributions of each taxon to between-habitat pair-wise Bray-Curtis dissimilarity (δ; range = 0–100%; $\delta = 0$ means that samples are identical) with the SIMPER ('similarity percentages') routine in PRIMER for fourth-root transformed and standardized invertebrate abundances. The percent contribution is the contribution of the taxon to the total average between-group dissimilarity ($\bar{\delta}$). The ratio $\bar{\delta}i/\mathrm{SD}(\delta i)$ is a measure of how consistently taxon i contributes to dissimilarity among all pair-wise sample comparisons. Taxa with a high ratio are good discriminating taxa for specific between-habitat comparisons (Clarke and Warwick, 2001).

We compared the biotic matrix for each habitat with matrices based on environmental variables ('matrix matching'). The PRIMER routine BVSTEP produces a rank correlation estimate—a Spearman coefficient (ρ_s)—between the Bray-Curtis similarity matrix for the biota and the normalized Euclidean distance matrix for the standardized environmental variables. BVSTEP finds the single variable that is most highly correlated with the biotic matrix and then adds the best additional variables using forward selection until the improvement in the correlation coefficient is <0.001. A high coefficient indicates that the ordination of the samples based on the biota qualitatively resembles the ordination of the sites based on the environmental data. Data from both randomly-selected and targeted sites were used in multivariate analyses.

RESULTS

Inter-habitat environmental variation

Principal components analysis of environmental data explained 72% of the variation among the sites (Figure 3A). There was high overlap of channel and shoreline sites which was not surprising since it is a well-mixed river with few tributaries. Exceptions included two channel sample sites from the Lake Oahe delta which were similar to backwater sites. A subset of backwater sites was similar to non-delta channel sites. Most of the variation (53%) among habitats and sites was explained by PC axis 1 which was positively correlated with dissolved oxygen (DO) and negatively correlated with temperature, turbidity and water-column chlorophyll *a* (Figure 3A). In other words, backwater sample sites were generally warmer, greener, more turbid, and had finer substrates than channel and shoreline samples sites (environmental data are summarized in an appendix to this paper). Principal component axis 2 explained only 19% of the variation, but separated two polluted backwaters from other backwater sites. These two backwaters were disconnected from the river and receive street runoff from Bismarck (T.R. Angradi, personal observation). We measured chloride and sulphate concentrations in them in excess of the North Dakota water quality standards for Class I streams (NDDOH, 2001). Substrate size (ϕ) was not as strongly correlated with any PC axis ($r = -0.64$ for PCA 1) as water quality measurements (Figure 3A) probably because of the greater overlap among habitats in substrate composition (the substratum at most sites included sand) than in water chemistry.

A PCA ordination including only backwater and channel sites but including more water chemistry variables revealed a similar two-dimensional pattern (Figure 3B): the two polluted backwaters were distinct; some backwaters were similar to channel sites, but most were distinct. In both PCA ordinations, backwater sites were much more variable in the ordinate space than the other habitats. We therefore hypothesized that variation in the macroinvertebrate assemblages would exhibit a similar among-habitat pattern of variation.

Inter-habitat variation in benthic assemblages

Non-metric multidimensional scaling (MDS) ordination (Figure 4A) showed that the channel assemblage was more variable in two-dimensional space than the other two habitats; a clear refutation of our hypothesis based on the PCA ordinations in Figure 3. As with the environmental ordinations, some channel samples from the Lake Oahe delta plotted among backwater samples.

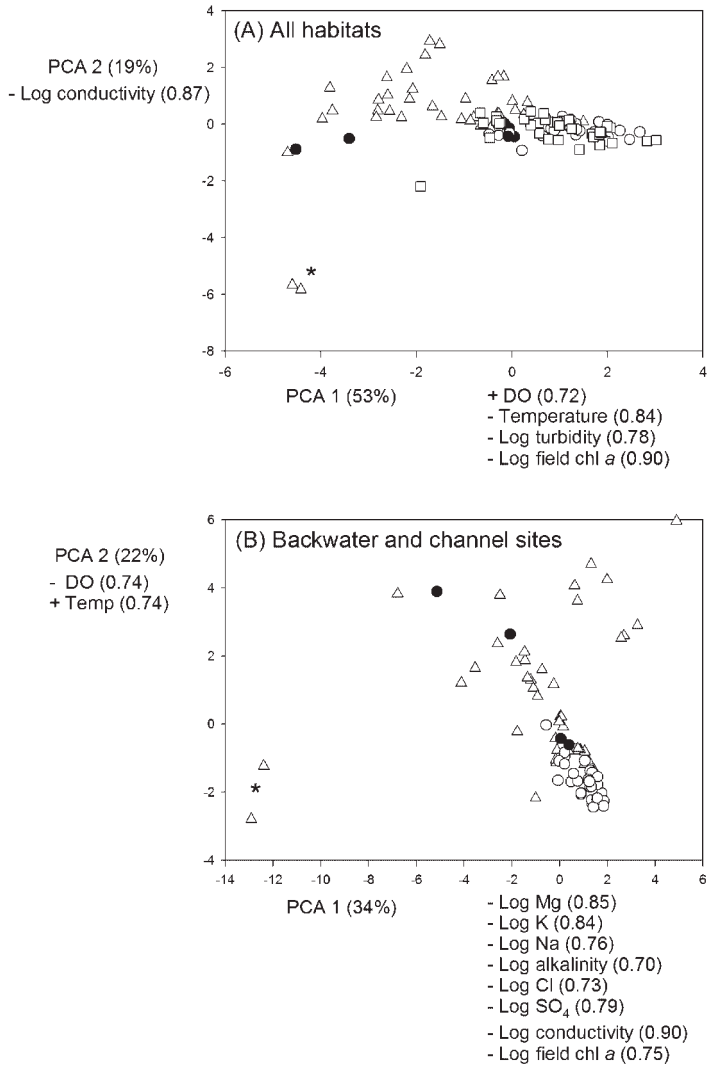

Figure 3. Principal components analysis (PCA) based on environmental data for Garrison Reach benthos sample sites. Input data for PCA of all habitats (plot A) included dissolved oxygen concentration (DO), water temperature, dominant substrate, conductivity, turbidity and chlorophyll *a* concentration from field flourimetry. Input data for PCA of backwater and channel sites (plot B) included the above variables and concentration of dissolved arsenic, copper, calcium, magnesium, nickel, potassium, sodium, chloride, zinc, total nitrogen, total phosphorus, total alkalinity, silica, sulfate and chlorophyll *a* from laboratory flourimetry (measurement units given in Appendix). Significant correlations ($r \geq 0.7$) between each axis and environmental variables are shown. All variables were log-transformed except DO, temperature and ϕ. Site revisits were excluded. Open circles, channel sites; filled circles, channel sites in the Lake Oahe delta; open squares, shoreline sites; open triangles, backwater sites. Asterisks denote two polluted backwater sites discussed in the text

The assemblage of all three habitats was dominated by Nematoda, Oligochaeta and Chironomidae. These groups comprised at least 80% of the mean abundance in all three habitats (Table I). Channel samples had fewer Oligochaetes and relatively more chironomids than samples from the other habitats. Although some chironomid genera were important in samples from all habitats (*Chironomus, Cladotanytarsus, Tanytarsus*), most chironomid genera varied in relative abundance among habitats. Some relatively abundant chironomid genera were found almost exclusively in one habitat: *Chernovskiia* and *Beckidia* in channel habitat, *Procladius* in backwaters.

Mean abundance was highest at backwater sample sites (16 671 m^{-2}; Table I caption), intermediate at shoreline sample sites (2 993 m^{-2}) and lowest at channel sample sites (1 690 m^{-2}). Among-sample variation in abundance

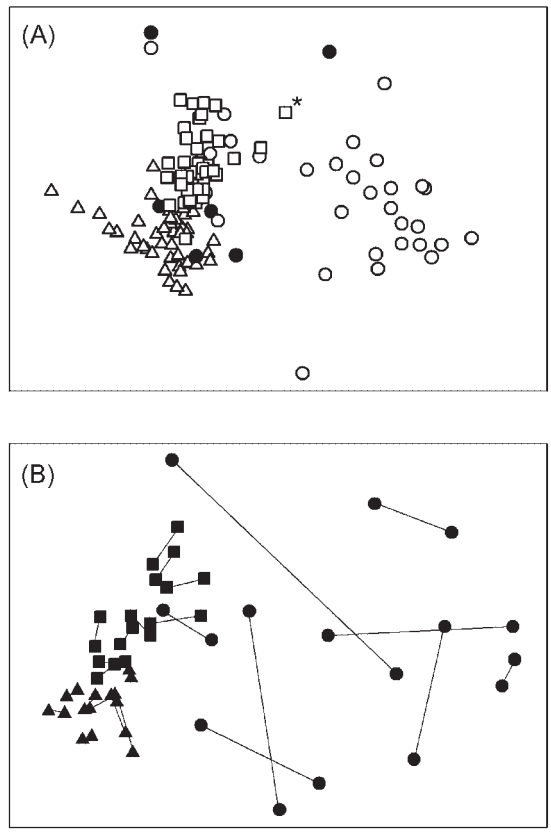

Figure 4. Non-metric multidimensional scaling (MDS) ordination of macroinvertebrate assemblage data for all Garrison Reach benthos samples (Plot A; minimum stress for 20 random restarts = 0.16; data were fourth root-transformed and standardized to relative abundances). Open circles, channel samples; filled circles, channel samples from the Lake Oahe delta; open squares, shoreline samples; open triangles, backwater samples. Asterisk denotes an outlier shoreline site discussed in the text. Plot B is the same ordination as Plot A with only samples from revisited sites shown. Lines connect site-revisit sample pairs. Filled circles, channel samples; filled squares, shoreline samples; filled triangles, backwater samples

was highest for channel sites (coefficient of variation = 310%; Table I caption) intermediate for shoreline sites (180%), and lowest for backwater sites (70%).

Average Bray-Curtis dissimilarity ($\bar{\delta}$) in the assemblages was highest between backwater and channel samples ($\bar{\delta} = 89$), followed by channel versus shoreline samples ($\bar{\delta} = 84\%$) and backwater versus shoreline samples ($\bar{\delta} = 70\%$; Table II). *Chernovskiia* (absent from backwaters), and Oligochaeta, Nematoda, *Chironomus*, and *Procladius* (more abundant in backwaters) accounted for most of the dissimilarity between backwater and channel samples. *Chernovskiia*, Nematoda, *Nais* (Naididae), *Cricotopus/Orthocladius, Hydra* (Hydridae), and Corixidae accounted for most of the dissimilarity between channel and shoreline samples. *Nais, Cricotopus/Orthocladius*, Tubificidae, *Chironomus*, *Procladius*, and *Dero* (Naididae) accounted for most of the dissimilarity between shoreline and backwater samples. Taxa that were consistently more abundant in one habitat than another (high value for $\bar{\delta}i/\mathrm{SD}(\delta i)$) and are therefore good discriminating taxa for specific between-habitat comparisons included Nematoda, which discriminated channel samples (where nematodes were rare) from other samples, and *Cricotopus/Orthocladius* (Table II) which discriminated shoreline samples from other samples. The dissimilarity between *a priori*-defined habitats was constrained by intra-habitat variation because for backwater and channel samples, there were groups of samples that were more similar to samples from other habitats than to the *a priori* habitat groups to which they belonged. We examine these intra-habitat groupings below.

Table I. Mean abundance (number of organisms m^{-2}) and relative abundance (percent of the total) of dominant taxa in samples from each of three habitats of the Garrison Reach of the Missouri River in North Dakota, USA. Values are for all sites excluding revisits. Mean (±SD) total abundance (number m^{-2}), coefficient of variation, and sample size: channel, 1690 ± 861, 310%, 37; shorelines, 2993 ± 885, 180%, 37; backwaters, 16 671 ± 1772 , 70%, 43

Channel		Shoreline		Backwater	
Taxon	Abundance (relative abundance)	Taxon	Abundance (relative abundance)	Taxon	Abundance (relative abundance)
Nematoda	517 (30.6)	Nais	1375 (46.7)	Nematoda	3552 (21.3)
Polypodium	172 (10.2)	Immature Tubificidae without capilliform setae	255 (8.5)	Immature Tubificidae without capilliform setae	3042 (18.2)
Nais	157 (9.3)	Immature Corixidae	167 (5.6)	*Nais*	1793 (10.8)
Cryptotendipes	143 (8.5)	Cricotopus/Orthocladius*	131 (4.4)	*Chironomus*	813 (4.9)
Chironomus	119 (7.0)	Nematoda	97 (3.2)	Aulodrilus	797 (4.8)
Immature Tubificidae without capilliform setae	80 (4.7)	*Hydra*	92 (3.1)	Immature Tubificidae with capilliform setae	511 (3.1)
Cladotanytarsus	56 (3.3)	Unknown Enchytridaeidae	71 (2.4)	*Dero*	382 (2.3)
Cryptochironomus	41 (2.4)	*Aulodrilus*	60 (2.0)	*Tanytarsus*	365 (2.2)
Immature Corixidae	37 (2.2)	*Chironomus*	59 (2.0)	*Cladotanytarsus*	356 (2.1)
Chernovskiia	28 (1.6)	*Cryptotendipes*	58 (1.9)	*Procladius*	335 (2.0)
*Cricotopus/Orthocladius**	25 (1.5)	*Limnodrilus*	47 (1.6)	*Limnodrilus*	298 (1.8)
Tanytarsus	24 (1.4)	*Trichocorixa*	45 (1.5)	Immature Coenagrionidae	261 (1.6)
Beckidia	23 (1.4)	*Paratanytarsus*	35 (1.2)	*Paratanytarsus*	224 (1.3)
Stempellinella	21 (1.2)	*Stempellinella*	32 (1.1)	*Enchytridaeidae*	222 (1.3)
Limnodrilus	21 (1.2)	*Tanytarsus*	31 (1.0)	*Caenis*	219 (1.3)
Aulodrilus	19 (1.1)	*Cladotanytarsus*	29 (1.0)	Planorbeidae unknown	209 (1.2)

*Larvae in these genera could not be reliably separated.

Table II. Contributions to average between-group (habitat) dissimilarity (δ) in sample composition based on Bray-Curtis dissimilarities. Mean Abundance (number of organisms m^{-2}, in habitat order from heading) follows taxon; channel values exclude Lake Oahe delta samples. T = <1 organism m^{-2}. Taxon in bold is the most discriminating for the comparison (highest value for δi/SD(δi))

Backwater vs. channel samples $\delta = 89\%$ (86% including Lake Oahe delta samples)		Channel vs. shoreline samples $\delta = 84\%$ (82% including Lake Oahe delta samples)		Backwater vs shoreline samples $\delta = 70\%$	
Taxon	Percent contribution	Taxon	Percent contribution	Taxon	Percent contribution
Chernovskiia (0, 33)	5.7	*Chernovskiia* (33, 0)	6.2	*Nais* (1793, 1396)	3.5
Immature Tubificidae wo cap. setae (3042, 33)	4.5	Nais (107, 1396)	5.3	***Cricotopus/Orthocladius*** (76, 131)	3.3
Nematoda (3552, 7)	4.3	*Cricotopus/Orthocladius* (26, 131)	3.9	Immature Tubificidae wo cap. setae (3042, 255)	3.2
Nais (1793, 107)	3.2	**Nematoda** (7, 97)	3.3	*Chironomus* (813, 59)	2.3
Chironomus (813, 25)	3.2	*Hydra* (6, 92)	2.8	*Procladius* (335,T)	2.3
Immature Tubificidae w cap. setae (511, 2)	2.9	Immature Corixidae (0, 167)	2.7	*Dero* (382, 8)	2.3
Procladius (334, 0)	2.8	*Cladotanytarsus* (44, 30)	2.7	*Aulodrilus* (797, 60)	2.3
Dero (382, T)	2.7	*Trichocorixa* (0, 45)	2.7	*Trichocorix*a (4, 45)	2.2
Aulodrilus (797, T)	2.6	*Limnodrilus* (18, 47)	2.7	Immature Tubificidae w cap setae (511, 9)	2.1
Limnodrilus (298, 18)	2.4	*Cyphomella* (14, 20)	2.6	Nematoda (3552, 97)	2.0

Between-visit variation

Between-visit variation in assemblage structure was highest for channel samples and lowest for backwater samples (Figure 4B). Separation between pairs of channel samples (original and revisit) from the same sample site (based on two-dimensional MDS ordination) exceeded total variation among sites for the other habitats. This result is not surprising given how dynamic the sand bed is in the channel of the Garrison Reach. Also, re-positioning and anchoring the boat over the same site coordinates as for the first visit was rarely possible in the swift-flowing Missouri.

Biological-environmental matrix matching and intra-habitat variation in assemblage structure

Step-wise rank correlations between the Bray-Curtis similarity matrix for the biota and the Euclidean distance matrix for the environmental site variables produced the combinations of environmental variables most highly correlated with assemblage structure for each habitat (Table III). For channel samples, a three-variable matrix including dominant substrate size (ϕ), depth, and log-transformed water-column chlorophyll *a* concentration produced the best match with the biotic matrix. Among the variables in the best combination for backwaters was

Table III. Combinations of environmental variables yielding the best matches of the macroinvertebrate assemblage and environmental similarity matrices for each habitat as measured by Spearman's rank correlation coefficient, ρ. Variable abbreviations: Distance = distance downriver from Garrison Dam, ϕ = dominant substrate particle size, phi scale, depth = sam-sample site depth, connectivity = backwater connected to Missouri River (yes or no), logSi = log-transformed water column Si concentration, logchl = log-transformed water column chlorophyll *a* concentration (laboratory), DO = water column dissolved oxygen concentration. Full set of environmental variables listed in the appendix

Habitat	ρ	Variables (in order added to model)
Channel	0.39	ϕ, depth, logchl
Shoreline	0.31	Distance, DO, ϕ
Backwater	0.44	Distance, DO, connectivity, ϕ, logCl, logSi

log-transformed chloride concentration which is considered a reliable indicator of local or watershed-scale human activity (Herlihy *et al.*, 1998). Dominant substrate particle size (ϕ) was included in models for all three habitats; distance from the dam and dissolved oxygen concentration were among the variables in the best matching combination for both backwater and shoreline samples. The correlation coefficients were low (<0.5), which we attribute to the relatively large number of biotic samples, which increased total variability among samples, and to our limited suite of environmental variables.

We included distance from Garrison Dam as a surrogate stressor gradient for flow regulation in the reach. For channel sites (excluding Lake Oahe delta sites), distance from the dam was rank correlated with dissolved oxygen ($\rho_s = -0.69$), temperature ($\rho_s = 0.76$), turbidity ($\rho_s = 0.66$), total N ($\rho_s = 0.52$), total P ($\rho_s = 0.57$) and total suspended solids ($\rho_s = 0.47$). For shoreline sites, distance from the dam was rank correlated with dissolved oxygen ($\rho_s = -0.49$), temperature ($\rho_s = 0.66$), and turbidity ($\rho_s = 0.54$). Summer water temperature increased about 1°C every 20 km downriver from the dam.

We plotted MDS ordinations for each habitat in which we highlighted selected 'explanatory' environmental variables from the biological-environmental matrix matching (Table III). A group of channel samples from 'clean' moving-sand substrates (no appreciable gravel or silt included) formed a distinct mesohabitat sub-grouping among channel samples (Figure 5A). Samples from this moving-sand group were dissimilar to other-substrate channel samples (Table IV), primarily due to the abundance of the predatory psammophilic chironomids *Chernovskiia* and *Beckidia*, which were characteristic of these moving-sand samples (Table IV), and oligochaetes which were rare in moving-sand samples. Sample depth distinguished the unique assemblages at the deepest sites (Figure 5B).

Table IV. Contributions to average between-group dissimilarity (δ) in sample composition for a posteriori groups of channel, backwater and shoreline samples. Mean abundance (number m^{-2}, in habitat order from heading) follows taxon; channel samples exclude Lake Oahe delta samples. $T \leq 1$ organism m^{-2}. Taxon in bold is the most discriminating for the comparison (highest value for $\bar{\delta}i/SD(\delta i)$). Only two unconnected backwaters were considered polluted

Moving-sand channel vs other channel samples $\bar{\delta} = 91\%$		Sandy silt (natural) vs. riprap shoreline samples $\bar{\delta} = 57\%$	
Taxon	Percent contribution	Taxon	Percent contribution
Chernovskiia (47, 0)	12.1	*Hydra* (25, 298)	3.3
Nais (T, 384)	7.4	***Trichocorixa*** (34, 80)	3.0
Beckidia (30, 13)	4.3	*Sigara* (8, 22)	2.8
Immature Tubificidae w cap. setae (1, 196)	4.1	*Limnodrilus* (60, 7)	2.6
Nematoda (T, 1273)	3.7	*Chironomus* (76, 7)	2.4
Hydra (4, 8)	3.7	Immature Tubificidae wo cap. setae (326, 33)	2.4
Cladotanytarsus (T, 135)	3.3	*Hydroptila* (15, 17)	2.3
Cricotopus/Orthocladius (T,135)	3.2	*Cricotopus/Orthocladius* (138,109)	2.3
Enchytridaeidae (T, 60)	3.0	*Cryptotendipes* (76, T)	2.3
Cyphomella (15, 16)	2.9	Immature Corixidae (220, 4)	2.3
Connected vs. unconnected backwater samples $\bar{\delta} = 61\%$		**Polluted vs. unpolluted unconnected backwater samples $\bar{\delta} = 64\%$**	
Aulodrilus (1248, 35)	3.0	*Cladotanytarsus* (1611; 646)	3.5
Immature Tubificidae wo cap. setae (2967, 3171)	2.7	Nematoda (82, 4, 202)	3.3
Nais (2649, 347)	2.6	*Chironomus* (1693, 542)	3.2
Cladotanytarsus (113, 767)	2.6	Coenagrionidae (0, 788)	3.1
Immature Coenagrionidae (7, 640)	2.4	***Cryptotendipes*** (144, 14)	2.8
Dero (486, 205)	2.3	*Polypodium* (827, 152)	2.8
Chironomus (887, 205)	2.3	*Microchironomus* (280, 5)	2.8
Immature Tubificidae w cap setae (509, 514)	2.2	*Nais* (0, 398)	2.8
Nematoda (3471, 3688)	2.1	Immature Tubificidae w cap setae (766, 479)	2.7
Cryptochironomus (150, 239)	2.0	Immature Tubificidae wo cap. setae (492, 3553)	2.6

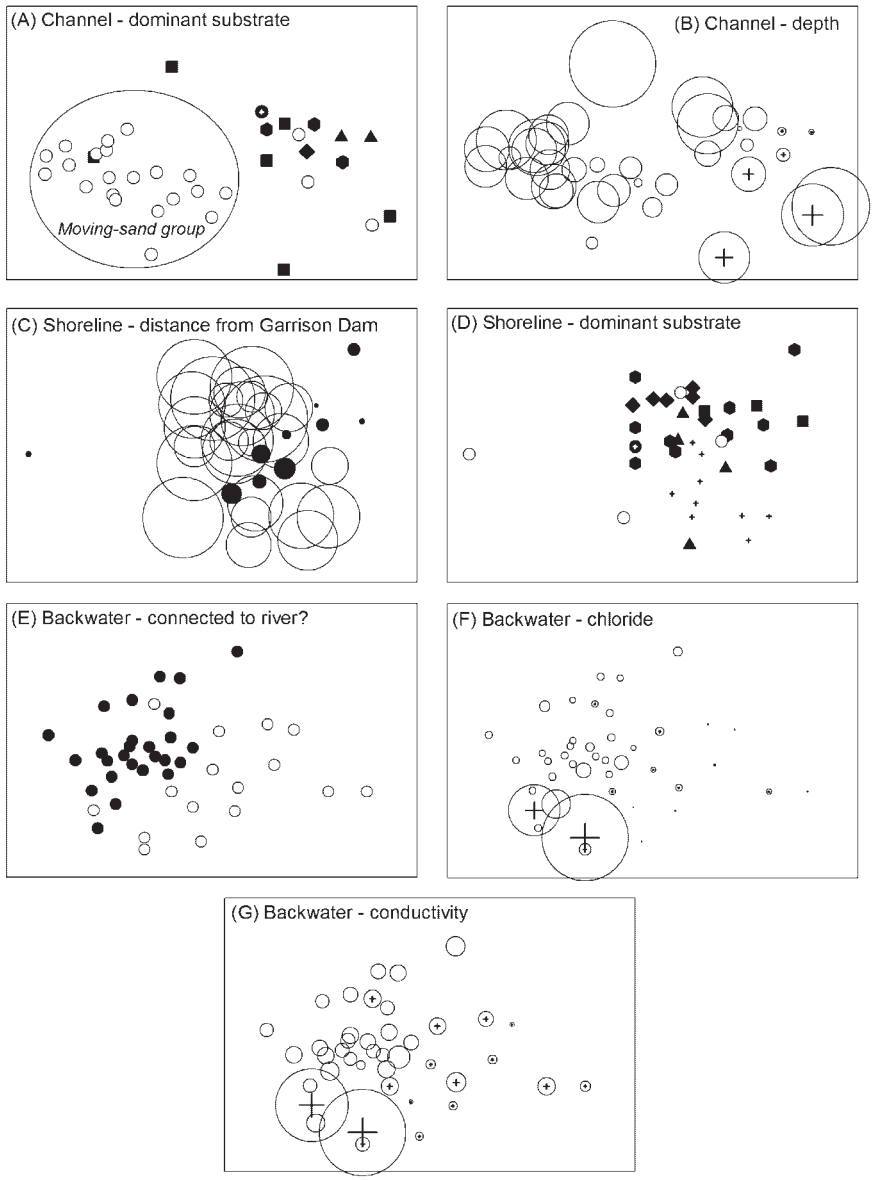

Figure 5. Non-metric multidimensional scaling ordination of macroinvertebrate assemblage data by habitat. In Plot A, symbols indicate ϕ for the dominant substrate. Samples inside circle are an *a-posteriori* group described in the text. Filled circle with plus, gravel or cobble ($\phi = -4.6$); open circles, sand ($\phi = 0$); filled square, sandy gravel ($\phi = -1.6$); filled hexagon, silty sand ($\phi = 2$); filled triangle, silt or clay ($\phi = 7.6$); filled diamond, sandy silt ($\phi = 4.3$). Plots B, C, F and G are scaled-symbol plots in which the symbol size is scaled to a percentage of the maximum value for all the samples to reflect the value of an environmental factor. Symbols in Plot B with a plus sign indicate samples from the Lake Oahe delta. In Plot D, symbols indicate ϕ for the dominant substrate (symbols as for Plot A except plus sign = rip rap ($\phi = -8.0$)). In Plot E, filled circle, connected backwater samples; open circle, unconnected samples. Plots F and G, symbols were scaled based on the untransformed water quality data. Symbols with a plus sign indicate samples from unconnected backwaters. Minimum stress for 20 random restarts was 0.15, 0.21 and 0.21 for channel, shoreline and backwater ordinations

Ordination of shoreline samples revealed an outlier (Figure 5C). This sample contained few organisms and plotted near the channel samples in the MDS ordination of all samples (Figure 4A; sample marked with an asterisk). This sample was collected just below Garrison Dam, but was dissimilar to other shoreline samples from near the dam. Daily stage fluctuations are greatest just below the dam and we may have inadvertently sampled recently exposed substrate at this site. In general, samples collected nearer the dam (small filled symbols in Figure 5C)

plotted near each other on the ordination relative to the overall range for shoreline samples. There was considerable overlap among samples from different shoreline substrates (Figure 5D). Samples from the coarsest substrate, riprap and gravel/cobble ($\phi = -8$), were only 59% dissimilar to finer substrate samples (Table IV). Among taxa contributing to the dissimilarity, *Hydra*, *Trichocorixa* and *Sigara* (Corixidae) and *Hydroptila* (Hydroptilidae) were more abundant in samples from rip rap, and *Chironomus*, Oligochaeta and immature Corixidae were more abundant in samples from natural sandy/silty shorelines.

With some exceptions, samples from backwaters connected to the river were dissimilar to samples from unconnected backwaters (Table IV, Figure 5E). *Aulodrilus* (Tubificidae), *Dero*, and *Nais* were more abundant in samples from connected backwaters; immature Tubificidae, Coenagrionidae and *Cladotanytarsus* were more abundant in unconnected backwaters. Scaling symbol size by chloride (Figure 5F) emphasized backwaters that were chemically distinct. The two backwater sites with the highest chloride concentration were the same backwaters identified as polluted by PCA (Figure 3). Average dissimilarity between these two backwaters and the other unconnected backwaters was 64% (Table IV). Most of the dissimilarity between the groups was accounted for by the greater abundance of *Cladotanytarus*, *Chironomus*, *Cryptotendipes*, and other Chironomidae in the polluted backwaters, and the lower abundance of Nematoda, Coenagrionidae and *Nais*. Although not included among the variables in the matrix matching combinations (Table III), we also scaled symbol size by conductivity (Figure 5G). The plot shows that connected backwater sites were similar overall, whereas unconnected sites included highly concentrated as well as chemically dilute sites.

Between-group dissimilarity values for additional comparisons between *a posteriori* intra-habitat groups (e.g. connected and unconnected backwater samples, moving sand and other-substrate channel samples; Table V) further highlighted affinities between groups of samples not apparent from plots of the *a priori* habitat classification (as in Figure 4A). For example, channel samples in the other-substrate group were more like (less dissimilar to) backwaters ($\bar{\delta} = 75$–79%) and shoreline samples ($\bar{\delta} = 66\%$) than moving-sand channel samples ($\bar{\delta} = 91\%$, Table V). Backwater and moving-sand channel samples were more dissimilar ($\bar{\delta} = 93$–95%) than backwater vs. other-substrate channel samples ($\bar{\delta} = 75$–79%). Unconnected backwaters were more dissimilar to shorelines than were connected backwaters ($\bar{\delta} = 74\%$ vs. 68%). A graphic depiction of these relationships (Figure 6) shows the strong influence of water velocity and substrate characteristics on the overall assemblage composition. Samples from the organic-matter-poor sand substrates in the channel were almost completely dissimilar ($\bar{\delta} = 95\%$) from the organic-matter-rich sandy silts of the lentic unconnected backwaters. Shoreline samples, which include several from riprap, had assemblages with an intermediate composition. In fact, a box drawn around the shoreline samples in the ordination (Figure 6) also encloses all of the other-substrate channel samples and more than half of the connected backwater samples.

Abundance and taxa richness for moving-sand channel samples was lower than for samples from other habitats (Figure 7). Abundance of organisms in channels samples was negatively rank correlated with near-bed current velocity (Figure 8). Moving-sand and other-substrate samples overlapped on the velocity gradient because some high-velocity sites had a gravelly bottom and some low-velocity sites had sand substrate (inundated sand-bar margins).

Table V. Average between-group dissimilarity ($\bar{\delta}$) in composition of benthic samples for *a-posteriori* groups of channel (excluding Lake Oahe delta samples unless specified), backwater, and shoreline samples. The most discriminating taxon was more abundant in the first habitat listed for each comparison

Comparison	$\bar{\delta}$ (%)	Most discriminating taxon
Moving-sand channel group vs. unconnected backwater	95	*Chernovskiia*
Moving-sand channel group vs. Lake Oahe delta (channel)	93	*Chernovskiia*
Moving-sand channel group vs. connected backwater	93	*Chernovskiia*
Moving-sand channel group vs. shoreline	91	*Chernovskiia*
Other substrate channel vs. unconnected backwater	79	*Nais*
Connected backwater vs. other substrate channel	75	*Cladopelma*
Shoreline vs unconnected backwater	74	*Nais*
Connected backwater vs. Lake Oahe delta (channel)	70	*Cladopelma*
Connected backwater vs. shoreline	68	*Cladopelma*
Shoreline vs. other substrate channel	66	Immature Corixidae

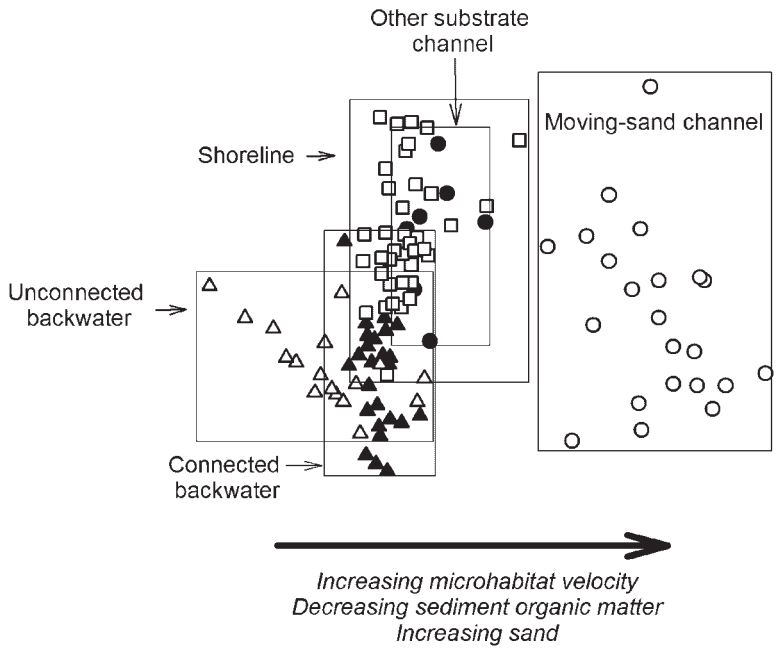

Figure 6. Non-metric multidimensional scaling (MDS) ordination of macroinvertebrate data for Garrison Reach benthos samples (minimum stress for 20 random restarts = 0.16; data were fourth root-transformed and standardized to relative abundances). Boxes surround samples in *a posteriori* groups. Plot is of same points in Figure 4A excluding Lake Oahe delta samples and one outlying other-substrate channel sample. Dissimilarity percentages (ϕ) among groups are given in Table V. Open circles, moving-sand channel samples; filled circles, other-substrate channel samples; open triangles, unconnected backwater samples; filled triangles, connected backwater samples; open squares, shoreline samples

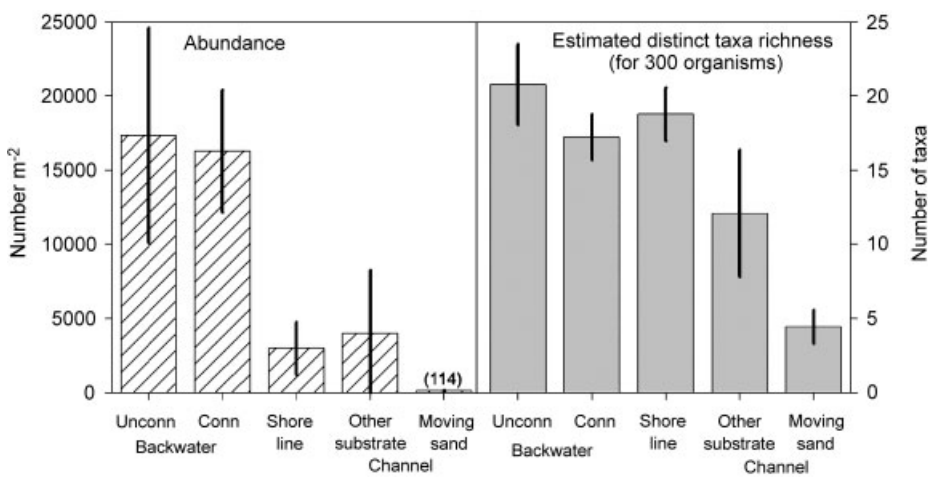

Figure 7. Sample means (±95% confidence intervals) for abundance and estimated distinct taxa richness by habitat including *a posteriori* channel and backwater groups. Mean abundance at moving-sand channel sample sites was 114 organisms m^{-2}. Other-substrate channel samples include samples from the Lake Oahe delta

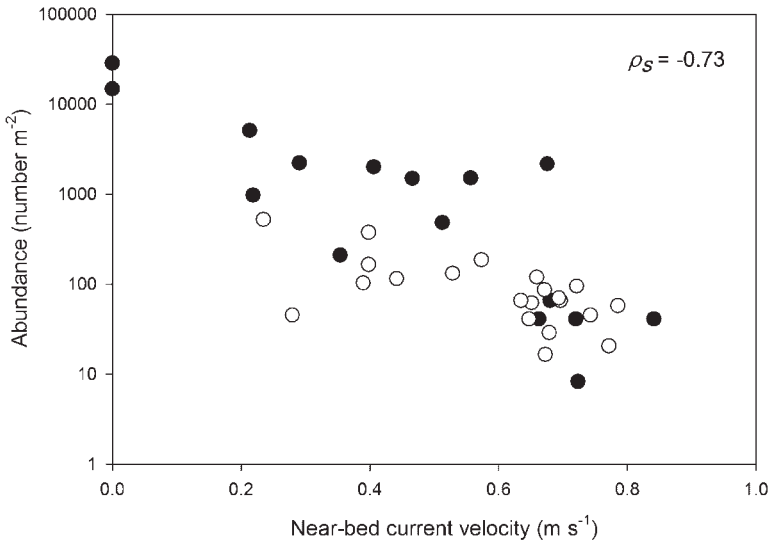

Figure 8. Association between near-bed current velocity and benthic abundance for all Garrison Reach channel sample sites, excluding samples from site revisits. Open circles, moving-sand sites assemblage; filled circles, other-substrate assemblages. The two zero-velocity Lake Oahe delta sites were excluded from calculation of the correlation coefficient. Note the log scale for abundance

DISCUSSION

Patterns of inter-and intra-habitat variation

Samples from moving-sand channel samples were not exclusively from sand (there was one PONAR sample that contained gravel), and there were three sand samples that did not have the moving-sand assemblage (two of them were from the Lake Oahe delta). Still, the pattern was distinct. We speculate that these samples reflect a depauperate, contagiously-distributed moving-sand assemblage that is restricted in the Garrison Reach to bed sands that are swept clean of silt and organic matter but do not generally include gravel. The psammophilic chironomids *Chernovskiia* and *Beckidia*, which were among the taxa most useful for discriminating moving-sand samples from other channel samples, were virtually absent in channel samples collected <30 km from the dam. Substrate in this section of the reach includes more gravel than downriver due to the substrate-coarsening effects of channel degradation (Williams and Wolman, 1984). This chironomid assemblage, which also includes *Robackia, Cyphomella*, and *Saetheria* in the Garrison Reach (at much lower densities than *Chernovskiia* and *Beckidia*), has been documented from channel habitat in the lower Mississippi River (Beckett *et al.*, 1983) and is apparently characteristic of large sand-bed rivers world-wide (Barton, 1980; Barton and Smith, 1984).

Unconnected backwaters in the Garrison Reach can be divided into three groups based on water chemistry: backwaters more dilute than the river, backwaters chemically similar to the river, and backwaters with a much higher ionic concentration than the river. Dilute, unconnected backwaters shared several characteristics; they were all small (<0.2 ha), surrounded by terrestrial vegetation, contained macrophytes, had low turbidity and contained no common carp (*Cyprinus carpio*)—evidence of a long interval since they were connected to the river and a general lack of disturbance. Unconnected backwaters that were chemically similar to the river usually had evidence of more recent connection to the river and were usually located in low spots in side channels that were dry at the time of sampling. The polluted (high ionic concentration) unconnected backwaters we sampled received untreated urban stormwater runoff from the city of Bismarck. Benthic assemblages at dilute and polluted unconnected backwater sites were generally distinct from most other backwater assemblages. Our findings corroborate Willemsen *et al.* (1990) and Trevino (1997), who showed that urban storm water runoff alters macroinvertebrate assemblages in retention ponds and other receiving waters.

Intra-habitat variation in assemblages for shoreline sites was less than we expected. We supposed that assemblages from riprap sites would be distinct from sandy or silty shorelines sites. There were some taxa that were

consistently more abundant in samples from riprap (e.g. *Hydra*, littoral Corixidae), but assemblage dissimilarity was relatively low ($\bar{\delta} = 57\%$) compared to other *a posteriori* intra-habitat groups. In the Garrison Reach, riprap is usually placed along outside bends where water velocity is highest. However, at kick sample locations within riprap, microhabitat velocity over and between the substrate is low and fine sediment is usually present (Barnum and Bachmann, 1988). So, although bank stabilization with riprap increases the local relative abundance of some taxa, it apparently does not cause the complete replacement of the natural shoreline assemblage.

Inter-habitat variation in the benthos of the Missouri River and other Great Rivers

Most previous studies of the benthos of the Upper and Middle Missouri River (above the Nebraska-Kansas border) have been comparisons among types of bank stabilization/channel training structures (Burress *et al.*, 1982, Atchison *et al.*, 1986) or comparisons between channelized and unchannelized reaches of the river (e.g. Morris *et al.*, 1968; McMahon *et al.*, 1972; Wolf *et al.*, 1972; Modde and Schmulbach, 1973; Nord and Schmulbach, 1973; Mestle and Hesse, 1993) rather than comparisons among habitats. Mizzi (1994) collected samples in several Garrison Reach habitats including the main channel, main channel border, connected backwater, secondary channel and tributary confluence. Burress *et al.* (1982) collected samples adjacent to a variety of Garrison Reach shoreline types including bank revetments, dikes and natural shorelines. These studies corroborate our general finding that the Upper Missouri River benthos was dominated by Chironomidae, Oligochaeta and Nematoda, and that main channel samples from moving sand had low benthic abundance and diversity. Like us, Mizzi (1994) found that abundance and diversity were highest in backwaters, lowest in the main channel, and intermediate in main channel border areas (similar to our shoreline habitat).

Available habitat-specific information for other Great Rivers generally corroborates our findings. Anderson and Day (1986) compared benthic assemblages in upper Mississippi River, USA, navigation pools for four habitats: channel, channel border, backwater and side channel. Like us, they found the variation among *a priori* habitats was obscured by intra-habitat variation associated with substrate size and presence of macrophytes. Beckett *et al.* (1983) sampled invertebrates in three lower Mississippi River habitats: natural banks (≈shoreline), permanent secondary channel (≈channel) and abandoned channel (≈backwater). Abundance and taxa richness was highest in the abandoned channel, intermediate on natural banks and lowest in the secondary channel. The benthic fauna was dominated by some of the same psammophilic chironomid taxa that were unique to our moving-sand channel samples. Marchese *et al.* (2005) examined three habitats in the Upper Paraguay River, Brazil: channel margin, central channel and floodplain lakes (≈shoreline, channel, backwater). Like us they found distinct assemblages in each habitat and higher local diversity in floodplain and bank habitats than in channel habitat.

Implications for Great River biomonitoring

Our findings have implications for designing a benthos monitoring program for a Great River ecosystem like the Missouri River. We conclude that a relatively comprehensive assessment of the Upper Missouri River could be accomplished by sampling three discrete aquatic habitats: unconnected backwaters, shorelines, and moving-sand channel areas. However, the three order-of-magnitude variation in benthic abundance we observed over the range of measured velocities, the low abundance and number of taxa, and the high variation in assemblage structure, suggest that detecting anthropogenic effects on channel assemblages of Great Rivers may be problematic. Exceptions include impoundment or other channel alterations that cause disproportionate changes in the benthic environment of the channel bed relative to shoreline habitat.

Based on patterns in overlap in benthos assemblages, we conclude that sampling the benthos of channel shorelines should capture much of the natural and stressor-induced variation in connected backwaters and channel habitat exclusive of moving-sand areas. In our study, lentic areas behind rock jetties or dikes projecting from the shoreline into the channel were considered backwater habitats. Reclassifying these highly-connected backwaters as main-channel shoreline and sampling them as such would increase the applicability of shoreline sampling for reach-scale Great River monitoring, but would also increase the total variation in shoreline assemblages. Poulton *et al.* (2003) suggest that lower Missouri River shorelines can be stratified into erosional and depositional habitats to improve sampling gear efficiency for patchily-distributed taxa likely to be sensitive to sediment contamination (e.g. burrowing mayflies).

Sampling shoreline assemblages has important practical advantages. Most reaches of Great Rivers of the Upper Mississippi River basin of the United States have well defined shorelines than can be safely sampled by wading (T.R. Angradi, personal observations), whereas backwater habitats are difficult to document *a-priori*, and are often deep and inaccessible by boat. Main-channel substrates in Great Rivers can be difficult to sample quantitatively, especially in lower reaches because of water depth and current velocity. Shoreline assemblages generally have a higher abundance and local diversity than channel assemblages and are comparable in diversity to backwater assemblages. Unlike main-channel habitat, a large number of organisms in many taxa can usually be collected with minimal effort by semi-quantitative kick sampling along Great River shorelines—a prerequisite for developing models and indices useful for routine bioassessment.

Whether unconnected backwaters or other off-channels habitats (e.g. floodplain lakes, tributary mouths) should be included in a Great River monitoring programme depends on the transverse spatial scale most relevant to river/floodplain management objectives. For example, sampling backwaters may not be necessary for assessing the condition of the main channel, but would be highly relevant for more holistic river ecosystem or floodplain assessment objectives (Mestle and Hesse, 1993). On the highly-regulated Garrison Reach, many unconnected backwaters are rarely reconnected to the Missouri River. As we have shown, however, their inclusion in the sample design may reveal otherwise hard to detect urban effects on the riverine hydroscape.

Great River sampling designs require insight into location of major habitat transitional zones. For example, by extending our channel sampling into Lake Oahe delta we increased total variation among channel sites. We excluded delta channel samples from much of our analysis because the habitat and benthic assemblage were more similar to backwaters than upriver channel sites.

CONCLUSIONS

Using multivariate analysis of assemblage data, we identified patterns of variation in the Garrison Reach benthic assemblage data. Such patterns may confirm or refute *a priori* classifications (in our case, the three original habitat types), and may suggest additional classifications or subclassifications of data relevant to sample design (in our case, the moving-sand channel assemblage and the unconnected-backwater assemblage). Multivariate patterns of variation may also suggest where combining habitats with high overlap in assemblage composition may increase monitoring efficiency (in our case, expanding the definition of shoreline habitat to include shoreline areas of connected 'backwaters' behind rock jetties).

The Missouri River ecosystem has been profoundly altered by >150 years of human disturbance (Galat *et al.*, 2005). All of these alterations affect, directly or indirectly, the distribution, structure and function of Great River habitats and their biota (Mestle and Hesse, 1993; Hesse, 1996). Therefore, any long-term great-river monitoring programme must select appropriate habitats to sample, and must anticipate the qualitative and quantitative changes in habitat that will occur as local and system-wide ecosystem restoration goals are realized (Thorp, 1992; Gore and Shields, 1995).

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APPENDIX

Means (SD) or medians for selected environmental parameters mentioned in the paper. Medians are for visually estimated parameters. Variation in sample size is due to missing data. Values are for sampled sites only and are not unbiased estimates for the Garrison Reach

Variable	Channel			Shoreline	Backwater	
	Lake Oahe delta sites ($n=4$–6)	Other substrate ($n=9$)	Moving-sand ($n=22$)	All sites ($n=37$)	Connected ($n=25$–27)	Unconnected ($n=16$)
Distance from Garrison Dam (km)	171.5 (2.3)	48.8 (45.3)	100.13 (40.7)	85.8 (49.0)	107.3 (42.5)	85.9 (36.9)
Dissolved oxygen (mgL^{-1})	9.4 (1.0)	11.11 (1.1)	10.4 (1.0)	10.3 (1.1)	8.2 (2.2)	6.3 (2.6)
Water temperature (°C)	20.1 (2.6)	12.1 (2.8)	15.3 (2.8)	14.9 (3.4)	19.0 (4.2)	23.1 (2.4)
Conductivity (mSs^{-1})	0.72 (0.1)	0.62 (0.1)	0.65 (0.1)	0.7 (0.1)	0.7 (0.1)	0.9 (1.0)
Turbidity (NTU)	36.2 (42.6)	4.1 (3.3)	5.6 (5.7)	4.7 (2.9)	11.0 (9.1)	11.0 (11.4)
Chlorophyll *a* from field measurements (μgL^{-1})	7.9 (9.8)	1.4 (0.5)	1.1 (0.5)	1.5 (0.9)	8.1 (16.7)	9.2 (11.6)
Chlorophyll *a* from lab measurements (μgL^{-1})	19.5 (33.2)	1.5 (0.3)	1.6 (0.7)	na	10.6 (16.2)	13.4 (16.3)
Median human influence score (0–19)	na	na	na	na	4	1
Sample depth (m)	1.7 (1.4)	2.4 (1.6)	2.0 (1.0)	na	1.4 (0.9)	0.6 (0.2)
Near-bed velocity $m\,s^{-1}$	0.35 (0.36)	0.51 (0.18)	0.59 (0.16)	na	na	na
Median substrate size (ϕ)	1	−1.6	0	2.0	4.3	4.3
Median substrate	Silty sand	Sandy gravel	Sand	Silty sand	Sandy silt	Sandy silt
Median backwater area (ha)	na	na	na	na	0.8	0.1
Arsenic (μgL^{-1})	4.3 (6.0)	1.8 (0.6)	2.7 (3.0)	na	1.9 (2.4)	13.9 (31.7)
Copper (μgL^{-1})	1.1 (0.5)	1.4 (0.4)	1.2 (0.5)	na	1.1 (0.8)	1.4 (1.1)
Calcium (mgL^{-1})	50.7 (2.3)	50.5 (3.2)	51.8 (1.9)	na	50.2 (8.4)	57.9 (64.4)
Magnesium (μgL^{-1})	22.1 (1.3)	21.0 (1.0)	21.3 (0.7)	na	22.5 (4.6)	37.1 (50.9)
Zinc (μgL^{-1})	7.4 (6.4)	4.5 (4.4)	6.0 (6.1)	na	13.2 (33.1)	9.7 (9.0)
Nickel ($\mu g\ L^{-1}$)	7.4 (7.1)	2.3 (4.0)	6.0 (6.0)	na	2.5 (3.9)	7.9 (6.5)
Potassium (mgL^{-1})	4.5 (0.7)	3.8 (0.3)	4.0 (0.3)	na	4.3 (1.0)	4.6 (3.1)
Sodium (mgL^{-1})	66.4 (16.9)	57.7 (4.4)	57.1 (5.0)	na	65.5 (27.0)	93.1 (152.1)
Chloride (mgL^{-1})	8.5 (0.9)	8.5 (0.3)	8.2 (0.4)	na	10.5 (5.2)	14.5 (27.2)
Silica (mgL^{-1})	5.9 (3.6)	6.7 (0.4)	6.5 (0.5)	na	6.2 (2.3)	5.5 (4.3)
Total alkalinity (mgL^{-1})	178.8 (25.0)	165.4 (5.3)	163.9 (6.7)	na	181.9 (50.6)	193.6 (141.6)
Total nitrogen (mgL^{-1})	0.7 (0.7)	0.2 (0.1)	0.3 (0.05)	na	0.6 (0.9)	1.3 (1.9)
Sulfate (mgL^{-1})	172.0 (18.0)	166.0 (5.2)	163.7 (6.6)	na	168.1 (28.4)	258.0 (441.0)
Total phosphorus (mgL^{-1})	0.07 (0.09)	0.01 (<0.01)	0.01 (0.01)	na	0.1 (0.1)	0.1 (0.1)
Total suspended solids (TSS, mgL^{-1})	25.5 (28.9)	2.2 (2.6)	5.1 (5.2)	na	10.3 (14.0)	11.8 (9.1)